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# Community Ecology

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# *COMMUNITY ECOLOGY*

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## *Abstract*

COMMUNITIES with *Microtus* tend to be structurally simple, usually grasslands or tundra, and to have no more than two species of *Microtus* and rarely more than six species of small mammals. *Microtus* often dominates both numerically and in total small mammal biomass, especially at higher latitudes. The small mammal community is most influenced by *Microtus* through its fluctuations in density, and thus also in biomass, by its relatively high level of diurnal activity, and by its year-round activity. Other species of small mammals may be adversely affected because *Microtus* usually is larger and behaviorally dominant and also because the mere presence of *Microtus* may focus predators on the area, especially during periods of high density. As generalized herbivores, primarily on grasses and herbs, *Microtus* has the potential to alter plant communities, either by selectively harvesting some species or through stimulating growth by grazing. Scarcely anything is known about the role *Microtus* plays in plant and small mammal communities, so both descriptive and experimental studies can make significant contributions to an understanding of the role and impact *Microtus* has on its communities.

## *Introduction*

*Microtus* always lives with other small mammal associates, whether in combination with one or more shrews, or cricetine, sciurid, heteromyid, murid, or other microtine rodents. Because it occurs primarily in temperate grasslands and in tundra (Getz, this volume), we anticipate that *Microtus* will usually be a member of

* Order of authorship determined by flip of a coin.

structurally simple plant communities, regardless of latitude. In North America, grassland and tundra (and often *Microtus*) are found between 35 and 70°N, and also in isolated montane and plateau regions of southwestern U.S. and northern Mexico (Hoffmann and Koeppl, this volume). In these ecosystems, *Microtus* often contributes as much as 90% of the biomass of small mammals at the location. Consequently, an understanding of the role of *Microtus* is essential to an understanding of the ecology and dynamics of the ecosystem. *Microtus* has been evaluated in the context of primary consumers in grasslands, as in the IBP studies reported by Birney et al. (1976), French et al. (1976), and Grant and Birney (1979).

*Microtus* most frequently has been studied at the population level (Taitt and Krebs, this volume). Population studies have reported in great detail the patterns of density, population growth and survival, reproduction, behavior, dispersal, and changes in gene frequency, among others. Such studies have included only one or at most two species of *Microtus* or perhaps another microtine rodent, under the assumption that the common patterns underlying cycles could be detected in all microtines. The population dynamics and interactions of syntopic non-microtines have largely been ignored in the intensive study of *Microtus* population biology. As a result, we know very little about the role of *Microtus* in the small mammal community; that is, how *Microtus* affects other small mammals and how other small mammals affect *Microtus*. Some investigators, notably Lidicker (1973, 1978), have suggested that microtines should be studied in the community context, but this admonition has not been universally accepted. Indeed, we found that the majority of papers on *Microtus* population biology do not even list the small mammal associates in the community.

In sum, small mammal ecologists have looked at least coarsely at the role of *Microtus* in some grassland and tundra ecosystems, and in great detail at the population biology of *Microtus*. But there are no reported studies of the role of *Microtus* in the community of small mammals living at specific locations.

In a sense, a chapter on the community ecology of a genus is almost without precedent, especially a genus with 23 species living in a wide variety of environments from Guatemala to northern Alaska. Our goal in writing this chapter is to evaluate the role of *Microtus* in a range of successional, latitudinal, and altitudinal environments in the context of other small mammals living with them,

and to explain the patterns of *Microtus* distribution and association in the context of evolutionary and historic events.

## *Communities of Small Mammals with* Microtus

### *Patterns of Geographic Distribution*

In general, mammals follow the biogeographic principle of having more species in the tropics and progressively fewer toward the poles (McCoy and Connor, 1980; Simpson, 1964; Wilson, 1974). Fleming's (1973) evaluation of forest-dwelling mammals at two locations at 65°N (15 and 16 species), 45 and 42°N (35 species each), and two locations at 9°N (70 species each) nicely illustrates this gradient of mammalian species in the New World. However, except at the extremes of latitude, small mammal communities do not follow this trend, for temperate and tropical grasslands, temperate forest, and tundra communities alike usually have six or fewer species (French, 1978). Instead of a gradient of numbers across the North American continent, numbers of small mammal species vary as much according to habitat type within climatic zones as across broad latitudinal zones. An even greater exception is the pattern of latitudinal gradients for the numbers of microtine, and, more specifically, *Microtus* species from the tundra to subtropical latitudes.

Numbers of species of *Microtus,* other microtines, and non-microtines for two north–south transects in North America are given in Table 1. Microtine species contribute more than 50% to the total rodent fauna north of 60°N in the western transect and north of 55°N in the eastern transect. South of 35°N, the number of *Microtus* species never exceeds one. Microtines other than *Microtus* are not found below 30°N along either transect. Thus, the trend of increasing numbers of species toward the tropics is strongly reversed for all microtine rodents, including *Microtus.*

Reasons for this reverse pattern of species diversity are many and varied, but originate in the biogeographic history of this exclusively Northern Hemisphere genus (Hoffmann and Koeppl, this volume). Given their northern origin, *Microtus* species tend to be well adapted physiologically, morphologically, and behaviorally to withstanding extreme cold and long winters, but are largely unable to with-

TABLE 1

NUMBER OF SPECIES OF *Microtus* COMPARED TO OTHER MICROTINES AND NON-MICROTINE RODENTS ALONG TWO NORTH-SOUTH TRANSECTS IN NORTH AMERICA (DATA FROM HALL, 1981)

| | End points of transects | | | | | |
|---|---|---|---|---|---|---|
| | 70°N, 14°W<br>15°N, 100°W | | | 70°N, 110°W<br>15°N, 90°W | | |
| Degrees N latitude | *Microtus* | Other micro-tines | Non-microtine rodents | *Microtus* | Other micro-tines | Non-microtine rodents |
| 70 | 3 | 4 | 2 | 0 | 2 | 0 |
| 65 | 4 | 4 | 6 | 1 | 3 | 1 |
| 60 | 2 | 4 | 8 | 1 | 6 | 4 |
| 55 | 1 | 4 | 8 | 1 | 4 | 5 |
| 50 | 4 | 4 | 15 | 1 | 4 | 7 |
| 45 | 4 | 4 | 18 | 2 | 3 | 14 |
| 40 | 2 | 4 | 16 | 2 | 3 | 12 |
| 35 | 4 | 3 | 27 | 2 | 2 | 14 |
| 30 | 0 | 1 | 33 | 1 | 1 | 11 |
| 25 | 0 | 0 | 25 | Gulf of Mexico | | |
| 20 | 1 | 0 | 25 | 0 | 0 | 16 |
| 15 | | | | 1 | 0 | 16 |

stand hot, arid conditions. Consequently, summer heat more than winter cold seems to determine the locations at which *Microtus* can live. Only *M. ochrogaster*, *M. californicus*, and, at some localities, *M. montanus* are found in grasslands that are hot and dry.

Although such folivores (leaf-eaters) as *Sigmodon* are an important part of tropical grassland communities, they contribute relatively much less to the total small mammal community there compared to the importance of microtine folivores farther north, where vegetative structure and diversity are much reduced and many fewer mammalian species are found. It is in the grasslands, tundra, and taiga habitats that one or a few microtine rodents dominate and may occur with a few species of insectivores (mostly shrews), carnivores (mostly weasels), and omnivores (such as *Peromyscus maniculatus*).

When the geographic ranges of all North American *Microtus* are superimposed on a single map (Fig. 1), it can be seen that at many localities only a single species of the genus occurs. In addition to certain islands, these general regions include much of northeastern

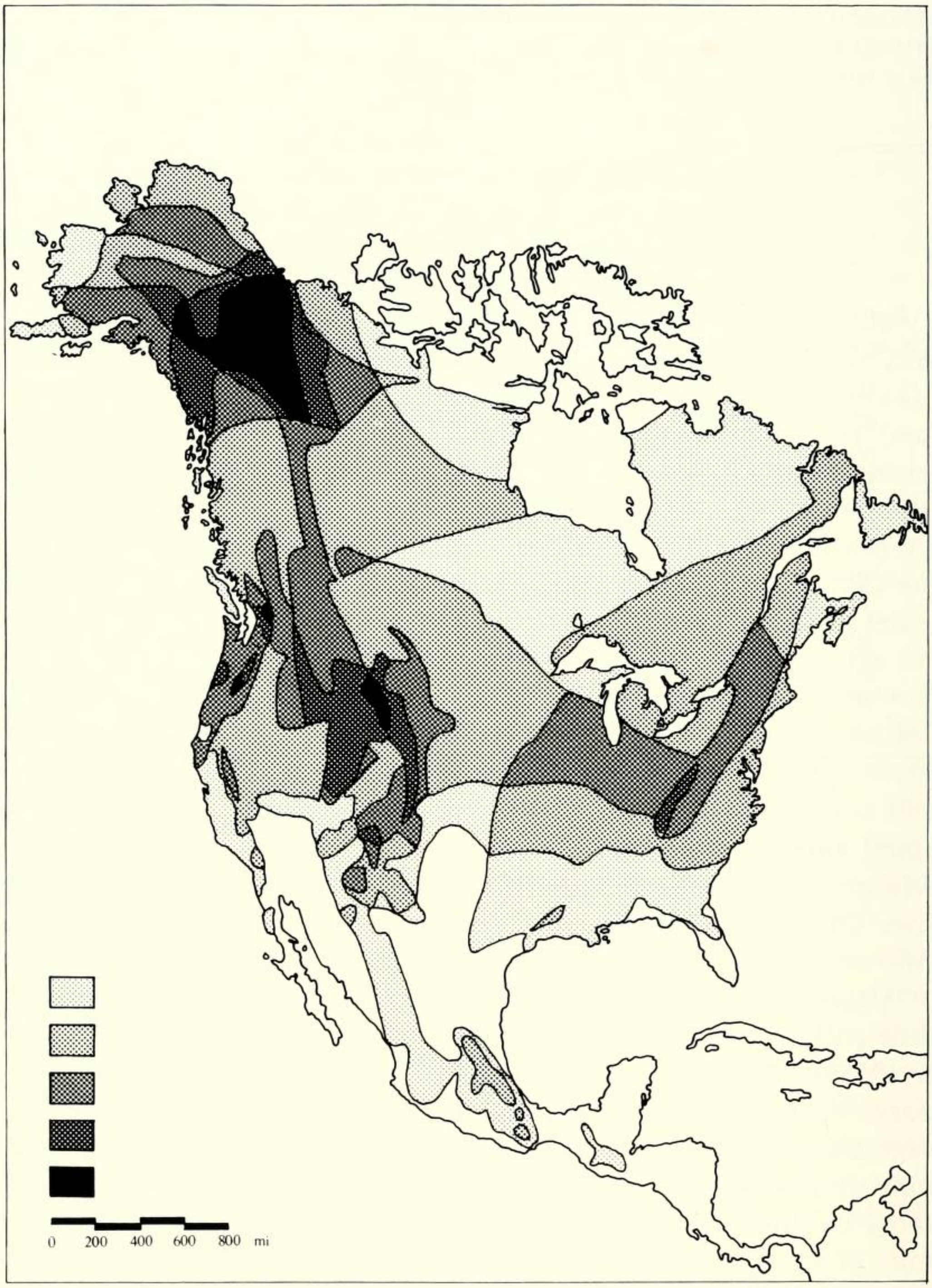


FIG. 1. Sketch map of North America showing approximate distributions of all species of *Microtus* in North America (compiled from Hall, 1981). Open areas indicate presence of no *Microtus* species. Stippling identifies areas that contain one (light stippling) to five (black) species of *Microtus*. Although as many as five or six species may overlap broadly, it is unusual for as many as three to co-occur in a single community.

Canada (*M. pennsylvanicus* being the only *Microtus*), southeastern U.S. (*M. pinetorum*), most of the range of the genus south of the U.S. (*M. mexicanus* and the relictual species *M. guatemalensis*; *M. quasiater*, *M. oaxacensis*, and *M. umbrosus* are sympatric and sometimes even syntopic with *M. mexicanus*), coastal areas of California and northern Baja California (*M. californicus*), and north-central Mackenzie Territory and sections of coastal Alaska (*M. oeconomus*). Other significant but small areas with only one *Microtus* species are western Kansas and adjacent Oklahoma (*M. ochrogaster*) and sections of New Mexico and Nevada (*M. longicaudus*). Two sympatric *Microtus* occur in much of the grasslands of the northern Great Plains and western Canada, where *M. pennsylvanicus* coexists with *M. ochrogaster*, *M. xanthognathus*, or *M. longicaudus*. Three and four broadly sympatric species tend to be limited to areas of considerable altitudinal relief and ecological diversity, including the Cascades, northern and southern Rockies, and parts of the Appalachians. The possibility of five *Microtus* species exists (on the basis of overlapping distributions only) for limited areas of the northern Rockies (mostly in Yukon) and the Cascades. Ranges of six species appear to approach each other closely in both the northern Cascades (*M. longicaudus*, *M. montanus*, *M. oregoni*, *M. pennsylvanicus*, *M. richardsoni*, and *M. townsendii*) and southern Cascades (*M. californicus* replaces *M. pennsylvanicus* as a possible sixth species). We know of no reports of more than three species of *Microtus* occurring together in a single small mammal community (see Getz, this volume). For example, even where Findley (1951, 1954) studied small mammal assemblages at Jackson Hole, Wyoming, no more than two of four species of *Microtus* were taken together in any of the 10 habitat types. Of the five *Microtus* in Colorado, Armstrong (1972) listed no more than three species for any of 14 community types. Possible triads were in yellow-pine woodland (*M. montanus*, *M. longicaudus*, and *M. mexicanus*), or montane subalpine meadow, highland streambank, and aspen woodland (*M. pennsylvanicus* replaces *M. mexicanus*). Steve West (pers. comm.) found three *Microtus* species together on only one of 25 study sites in central Alaska; that site, a recently burned black-spruce forest, also had three other microtine species. A total of six syntopic microtines is high, but non-*Microtus* species (for example, *Synaptomys* sp., *Clethrionomys* sp.) commonly occur with one or two species of *Microtus*.

The increase in small mammal species diversity in areas char-

acterized by great altitudinal relief is well known, and the importance of this pattern to studies of latitudinal species diversity was reiterated recently by McCoy and Connor (1980). Its importance specifically to *Microtus* species was demonstrated for *M. longicaudus, M. pennsylvanicus, M. montanus,* and *M. mexicanus* in New Mexico by Findley (1954, 1969) and Findley and Jones (1962). Armstrong (1972:Fig. 121) illustrated the relationship between mammalian species density and mountainous regions in Colorado (see also Table 1).

In sum, communities with *Microtus* tend to be grasslands or tundra, and rarely to have more than two species of *Microtus* or six species of small mammals overall. Thus, their habitats tend to be structurally simple and the number of co-occurring species few. *Microtus* often dominates numerically and in its contribution to total small mammal biomass.

### *Environmental Parameters*

Despite the fact that one or another species of *Microtus* can be found over most of North America, voles sometimes are restricted locally, and thus are not a ubiquitous component of North American grasslands and tundra. Many interrelated environmental parameters undoubtedly contribute to their presence or absence in a given community, including weather and climate, vegetative structure, food availability, competition, and predators.

*Weather and climate.—Microtus* is poorly adapted to conserve water or to thermoregulate at high ambient temperatures (Wunder, this volume). No *Microtus* species is found strictly in deserts or even desert grasslands. In southwestern Kansas, where *M. ochrogaster* reaches its southwestern distributional margin in relatively arid shortgrass prairie, this vole utilizes apparently self-dug burrows and is almost exclusively nocturnal during summer, presumably to avoid the extreme daytime heat and desiccating wind (Birney, pers. observ.). The short tail and ears and dense fur of *Microtus* serve well to conserve heat, but not to dissipate it.

In contrast, most or all species of *Microtus* are able to persist and even thrive in extremely cold climates. For example, *M. oeconomus* and *M. miurus* occur exclusively in the subarctic and tundra of northwestern Canada and Alaska. *M. xanthognathus, M. pennsylvanicus,* and *M. longicaudus* also extend their distributions inside

the Arctic Circle. Although the air temperature may be as low as −70°C, the subnivean environment of the vole is close to 0°C. Winter survival of some species is enhanced in part by their habit of communal nesting. *M. xanthognathus* in central Alaska constructs large middens of stored food and insulation for winter survival of the five to 10 occupants (Wolff, 1980). Communal winter nesting is known for other species as well, including *M. pennsylvanicus* in New York (Madison, this volume) and *M. ochrogaster* in warmer eastern Kansas (Fitch, 1957).

Local weather conditions probably rarely affect the occurrence of voles in most small mammal communities, except indirectly through an effect on the vegetation. Martin (1960) reported that in the mixed prairie of western Kansas, *M. ochrogaster* was at low density during one drought and high density during another, indicating that even prolonged aridity does not invariably reduce the abundance of the species. However, on Martin's study area (a western wheatgrass community) the highest density recorded in two years was only 18.4 voles/ha, a much lower density than the 160 or more per ha reported for the same species in ungrazed tallgrass and in irrigated and fertilized shortgrass (Birney et al., 1976). Gaines and Rose (1976) reported densities of prairie voles of about 180/ha from brome oldfields in eastern Kansas. Thus, although vole populations can survive and apparently even thrive during temporary periods of drought, their role in the small mammal community of such areas may be relatively less than in areas of greater or more regular rainfall.

*Flooding.*—Flooding is a potentially serious short-term environmental factor that could affect small mammal communities. Voles are not adapted to climbing emergent vegetation, as has been observed for such rodents as *Peromyscus* and *Oryzomys* during floods. Wolff (1980) concluded that the flooding of old winter nests did not adversely affect *M. xanthognathus* because they dispersed at the time of snow melt. Similarly, Bee and Hall (1956) described the periodic flooding of the burrows of *M. miurus*, but the voles apparently were not excluded from the community by the temporary flooding. *M. pennsylvanicus* has been reported to avoid saturated substrates (Getz, 1967), but Lyon (1936) reported this vole living in grass tussocks surrounded by water in Indiana swamps. In peatland fens in northern Minnesota, Birney (pers. observ.) has studied

breeding populations of *M. pennsylvanicus* living on sphagnum hummocks surrounded by standing water. Harper (1956) judged that a few hours of flooding during spring "break-up" in Keewatin had little effect on a population of *M. pennsylvanicus,* but that flooding and subsequent freezing on the same meadow in November greatly reduced their chances for winter survival.

*Substrate.*—*Microtus* species invariably use subterranean burrows to one degree or another. Soil richness and texture undoubtedly affect the local distribution and abundance of all species indirectly depending on their ability to burrow. Only for the fossorial species, *M. pinetorum,* has this been clearly demonstrated. Fisher and Anthony (1980), studying woodland voles in Pennsylvania orchards, failed to find them in one orchard with soils having relatively low percentages of gravel and sand and high percentages of fines and silts. They concluded that soil texture strongly influences the distribution of *M. pinetorum,* which requires more than 35% gravel and 20% clay, and less than 65% fines and 40% silt together with between 25 and 48% sand. In less-disturbed woodland habitats, this vole may burrow primarily in the duff and upper humus layers, and thus may be less rigidly tied to soil texture than to the surface covering.

Soil moisture may be of considerable importance, but how much of this is directly related to moisture and how much is indirect as moisture affects vegetation has not been determined. Murie (1969) showed that *M. pennsylvanicus* favored wet over dry substrates in the laboratory, but that *M. montanus* from the same area showed no preference. Getz (1967), on the other hand, found that *M. pennsylvanicus* avoided saturated substrates in the laboratory.

*Microtus ochrogaster* occupies burrows dug in hard, dry loam over much of its range, but most burrowing activities take place following autumnal rains that increase the friability of the soil (Rose, pers. observ.). Wolff and Lidicker (1980) noted that the complex, branching burrow systems of *M. xanthognathus* penetrated 15–25 cm, that is, to mineral soil or permafrost. Populations of *M. pennsylvanicus* on the Anoka Sand Plain of Minnesota reach high densities in the tall marsh grasses that grow there, but we know of no places where dry sand serves as a suitable substrate for *Microtus.* In Keewatin, Harper (1956) found *M. pennsylvanicus* in riverside meadows, sedge bogs, and on grass-covered sand dunes but never on the open summits of the gravelly ridges in the Barrens.

Rocky soils in mountainous areas serve as suitable substrates for voles of several species. For example, the usual habitat of *M. chrotorrhinus* seems to be the edges of boulder fields, although rock voles are sometimes found in unburned clearcuts (Kirkland, 1977), where limbs and brush piles may substitute for rocks.

*Vegetation.*—We believe that vegetation, more than any other single environmental factor, determines the presence or absence, as well as the relative role and importance of *Microtus,* in small mammal communities. Two field experiments on *M. ochrogaster* show the dramatic effect of increasing vegetative cover on this species. Birney et al. (1976) excluded cattle from grazing a 1-ha plot of tallgrass prairie in northeastern Oklahoma and observed the vole population increase dramatically during a single summer from none in May to 24 individuals/ha in October, while standing crop vegetation increased from 230 to 400 g dry weight/$m^2$. Only an occasional vole (1.0/ha) was trapped in an adjacent grazed control in October. Grant et al. (1977) provided irrigation water and nitrogen to two 1-ha plots of shortgrass prairie in eastern Colorado and compared the small mammal communities to those on initially similar controls. Over 4 years, *M. ochrogaster* located and became established on the experimental grids, showing a pattern of increasing from relatively low densities each spring to successively higher and earlier peak densities (over 100/ha in the fourth year) each summer or autumn. By comparison, no voles were trapped on the control grids until the third year of the study, and permanent populations never became established there. Cover levels on the experimental plots fluctuated between 600 and 1,200 g of dry weight/$m^2$, compared to 300–600 g/$m^2$ on the controls. Abramsky and Tracy (1979) speculated that shortgrass prairie is unsuitable for *M. ochrogaster* under conditions of normal rainfall and fertility; sparse vegetation and summer heat probably limit the distribution (Fig. 1) of these populations.

Birney et al. (1976; also see Elton, 1939; Frank, 1957; Getz, 1971) discussed several attributes of vegetative cover for *Microtus.* Of perhaps greatest importance is concealment and protection from predators. Getz (1970) concluded that heavy predation on a population of *M. pennsylvanicus* following mowing and baling of the vegetation accounted for the loss of most individuals, although his trapping results suggest that a few may have moved into an adjacent unmowed field.

Food provided by the vegetation obviously is also of great importance. Bee and Hall (1956), who studied the community association of five microtine species in northern Alaska, found that each species was associated with a particular vegetation type. Studies by Jung and Batzli (1981) demonstrated that secondary plant compounds differentially affected the growth rates of arctic microtines, and thus that the mere presence of green forage, even though it might provide adequate cover, is not synonymous with the presence of high-quality food for microtines. For most *Microtus* species, however, especially those that occur in vegetatively diverse habitats, a wide range of food is eaten (Zimmerman, 1965), and thus the species composition of grassy habitats is often of less importance to *Microtus* than is the presence of adequate cover (except see Batzli, this volume).

The presence of vegetative cover also must affect behavioral interactions among conspecifics. For example, Warnock (1965) demonstrated that cover reduced both fighting and mortality of crowded captive *M. pennsylvanicus*. Furthermore, the protection provided by dense cover undoubtedly permits daylight activity, which could be especially important for species living at high latitudes where daylight periods are long or even continuous during summer.

Hopkins (1954) measured the effects of a mulch layer in grassland habitat, and demonstrated its effect on the microhabitat. Such factors as surface-level humidity, temperature, penetration of light, and soil moisture all are affected by cover. Additionally, heavy cover prevents dense packing of snow at ground level, thus making the subnivean space more hospitable to the small mammals that live there.

Grant et al. (1982) demonstrated that cover levels on four grassland study areas had a greater effect on herbivorous rodents than on omnivorous or granivorous ones. Removal of cover by grazing ungulates affected the three most important herbivorous small mammals (*M. montanus, M. ochrogaster,* and *Sigmodon hispidus*) more adversely than any of the other eight common rodents. These results were interpreted as strong support for the hypothesis (French et al., 1976; Grant and Birney, 1979) that the general composition of grassland small mammal communities is determined primarily by structurally simple attributes (including cover) of the habitat. This hypothesis appears to be especially applicable to communities with one or more species of *Microtus*.

Not all species of *Microtus* are restricted to structurally simple grassland and tundra environments. Wolff and Lidicker (1980) pointed out that *M. xanthognathus* is restricted to the taiga. Within this broad habitat type, taiga voles appear to utilize a wide variety of forested and grassland areas from burned to unburned black-spruce forest to wet, grassy swamp. However, West (1979) found *M. xanthognathus* primarily in grass-sedge habitat associations with early successional stages, and considered *M. oeconomus* to have the widest habitat use pattern of Alaskan *Microtus*. Whitney (1976) also studied populations of *M. oeconomus* in vegetationally diverse taiga near Fairbanks, Alaska, but considered the species to have a narrower niche than sympatric *Clethrionomys rutilus*. Bee and Hall (1956) found *M. miurus* in a variety of wet and dry habitats, but usually associated with willows, on which it seemed to be partially dependent for winter food. *M. pinetorum,* commonly found in eastern deciduous forest, seems to reach high population densities only in grassy orchards (Benton, 1955), sometimes in the presence of *M. pennsylvanicus* (Fisher and Anthony, 1980). Additional evidence that grasses can enhance habitat quality of woodland voles was provided by Gentry (1968), who studied a population of *M. pinetorum* within enclosures in a *Lespedeza-Andropogon* oldfield in South Carolina, where trees were absent. Findley (1951) found *M. longicaudus* on forested rocky hillsides, in alder-willow swamps, and in grassy, open woods. Armstrong (1972) found long-tailed voles in a wide variety of habitats including sagebrush and pine woodland in Colorado. Other species that may be found in forested habitats include *M. pennsylvanicus,* especially in open woodlands with a grassy floor and on small islands (Cameron, 1958); *M. montanus,* but only if grass is available; *M. richardsoni,* in association with mountain streams and alpine marshes; *M. oeconomus,* present in all but the most mature black- and white-spruce forest in Alaska (West, 1979); and *M. oregoni,* which lives in a variety of habitats including damp areas within redwood, fir, spruce, and hemlock forests (Ingles, 1965).

*Competition.*—Despite the fact that there have been few studies of competition in *Microtus* (for example, Conley, 1976), we see competition as being very important in the shaping of communities with *Microtus*. There are many examples of *Microtus* numerically dominating other species, many of which have been given in this chapter. The most dramatic are those in which voles, such as *M.*

*pennsylvanicus,* outnumber all other small mammals combined, and may contribute more than 90% to total small mammal biomass (French, 1978; Pruitt, 1968). At some locations, two species share a prominent role in the community, such as in the central U.S. where *M. ochrogaster* and *M. pennsylvanicus* overlap in distribution (Krebs et al., 1969). At others, such as in eastern Kansas, *M. ochrogaster* shares the herbivore role with *Synaptomys cooperi,* another microtine rodent and a presumed ecological equivalent (Gaines et al., 1979) or with the larger cricetine, *Sigmodon hispidus* (Rose et al., 1977).

It is clear that *Microtus* is a dominant herbivore of northern origin and affinities and that *Sigmodon* is a dominant herbivore in grasslands from Mexico northward into the central plains. *S. hispidus* has moved progressively northward during historic times, and its movement across Kansas and into Nebraska has been documented by Genoways and Schlitter (1966). In part, this colonization northward was due to the ability of *Sigmodon* to use disturbed areas and perhaps cropland (Fleharty and Olson, 1969), but also to its ability to respond to semiarid conditions such as occurred during the 1930's "dustbowl" era. Droughts have a strongly adverse effect on *Microtus* (Martin, 1960; French et al., 1976), and this climatic factor may have contributed to the replacement of *M. ochrogaster* by *Sigmodon* as the dominant folivore in the grasslands of Kansas and perhaps of neighboring states as well. Some investigators (for example, Glass and Slade, 1980; Terman, 1974) have attempted to study competition between *Sigmodon* and *M. ochrogaster,* using combinations of field and laboratory experiments. *Sigmodon* tends to win under the conditions used in these studies. A counterbalancing force is high winter mortality in *Sigmodon,* which is poorly adapted to severe winters (Fleharty et al., 1972). There is good evidence that local populations of *Sigmodon* go extinct during severe winters (Slade, pers. comm.), at least in eastern Kansas. We imagine that such events would happen with greater frequency the farther north the populations. Thus, in this example of intergeneric competition of the dominant small herbivores in the central plains, it seems that *Microtus* contends better with the winters and *Sigmodon* with both summers and drought. Baker (1971) provided several examples of pairs of *Sigmodon* species that coexist in the Mexican grasslands in much the same way that pairs of *Microtus* do north of 35°N.

Competition has been proposed as the mechanism that tends to separate two or more coexisting *Microtus*. Findley (1951, 1954), in some of the earliest examples of possible biological competition in vertebrates, never found more than two of four *Microtus* species at the same location near Jackson Hole, Wyoming. The association between *M. montanus* and *M. pennsylvanicus* also has been studied by others, including Douglass (1976), Hodgson (1972), Koplin and Hoffmann (1968), and Murie (1969, 1971), using both laboratory and field experiments. Despite the numerous examples of possible competitive interactions of two *Microtus,* Krebs (1977) was unable to find any evidence that *M. ochrogaster* and *M. pennsylvanicus* had negative effects on one another. Nor could Gaines et al. (1979) find evidence that *M. ochrogaster* and *Synaptomys cooperi* adversely affected one another.

One of the most interesting examples of how competition may be important in shaping small mammal communities is found in the distributional patterns of *M. pennsylvanicus* and *Clethrionomys gapperi* in the islands of the St. Lawrence River and off the east coast of mainland Canada. In parts of the Maritime Provinces, *Clethrionomys* is absent, probably due to events of the post-Pleistocene period. There *M. pennsylvanicus* occupies a much wider range of habitats than is considered typical of that species, including interior forest habitats far removed from patches of grasses (Cameron, 1964). On islands in the St. Lawrence River, some of which have become connected with the mainland during historic times, some have *Microtus* and others have *Clethrionomys*. The species present lives in a wider range of habitats than would be characteristic on the nearby mainland where the two occur together. Cameron's explanation is that chance has played a role in determining which species colonized an island, but that once established the resident species was able to prevent successful colonizations by the other. Two later studies of this pair of microtines (Iverson and Turner, 1972; Turner et al., 1975) reported their winter coexistence, first in grassland habitat and then in spruce forest. In each case, when aggression levels increased with the onset of the reproductive season, the species that seemed to be in the "wrong" habitat left to return to its typical habitat. During the second study, Turner et al. (1975) used behavioral studies in the laboratory to determine that, although it dominated behaviorally throughout the winter, *Microtus* still was excluded by *Clethrionomys* from the forest habitat when breeding

resumed. They interpreted these studies as competitive habitat exclusion related to reproduction-associated aggression. In a 10-year study of these two microtine rodents and *Peromyscus maniculatus* on islands in Maine, Crowell (1973) implicated competition as the principal reason for *Microtus* dominating the other two in nature.

*Microtus pinetorum* usually lives at low densities in disjunct populations in eastern deciduous forests. However, in orchards (Benton, 1955; Byers, this volume) or in enclosures where competitors are absent (Gentry, 1968), it can reach much higher densities. It is unclear how *M. pinetorum* responds to competition by *M. pennsylvanicus* but such studies are now in progress in orchards. *M. pinetorum* may be restricted mostly to forests because its poor competitive abilities prevent it from thriving elsewhere. If so, we would expect it to be displaced by *M. pennsylvanicus* in orchards.

Determining the role of competition in structuring communities with *Microtus* will require a combination of approaches including field experiments in which pairs of *Microtus* species coexist in some plots and live as separate species in others. Grant (1972) has conducted such studies with pairs of different species, including *Microtus,* in Ontario. Studies such as Getz (1963), of the renal efficiencies of *M. ochrogaster* and *M. pennsylvanicus,* and Zimmerman (1965), of the food habits of the same species, will be particularly useful in evaluating why species may be living syntopically in some places and not at others. Radiotelemetry and radio-isotopic techniques undoubtedly will be very useful in evaluating the microdistributions of individuals of the same and related species. We emphasize the need to have the non-*Microtus* rodents included as a part of these experiments because the evaluation of their role may be crucial to the proper interpretation of the results of all community studies.

*Predation.*—The importance of predation in population regulation and in determining the composition of small mammal communities has long been debated. Interactions between predators and *Microtus* species, considered in depth elsewhere (Pearson, this volume), may be relatively important under some circumstances in determining the magnitude of the impact of *Microtus* in the total small mammal community. Both mammalian (Pearson, 1971) and avian (Korschgen and Stuart, 1972) predators feed regularly and heavily on *Microtus* when they are available.

Pearson (1964:Fig. 2) clearly demonstrated the high percentage

of a population of *M. californicus* that could be accounted for in predator scats as the vole population declined from August of one year until March of the next. Similarly, Maher (1967) observed evidence on Banks Island, Northwest Territories, that *Mustela erminea* had killed all but a few lemmings (both *Dicrostonyx* and *Lemmus*) on the island during winter after the lemming populations had been at least moderately high the previous autumn. Pearson (1971) concluded that predators have a major impact on microtine populations, especially following a "crash," when the presence of secondary prey species enables carnivores to exert heavy predation pressures on the remaining low population of voles. We concur with this conclusion, and suggest that such predator pressure may result in lower biomass and higher species diversity of the small mammal community than might otherwise exist. However, at moderate or high population densities, especially during periods of recruitment, we doubt that predators have much impact on the *Microtus* component of the community (see Golley, 1960).

## *The Influence of* Microtus *on Communities*

*Microtus* influences its plant and animal communities because of frequently great density, relatively large size among small mammals, and indirectly because of high metabolic rates. In the extreme, these combine to produce denuded habitats during *Microtus* plagues, but more typically *Microtus* is a prominent, if not always dominant, member of the small mammal community. Its effects on plant communities are largely unmeasured but high differential consumption of some plant species may affect the relative success of plant species and thereby alter the habitat sufficiently to affect the animal component of the community.

The small mammal community with *Microtus* is often more variable than, for example, desert rodent or forest mammal communities, which typically lack *Microtus*. The latter communities have a high proportion of nocturnal species, and their numbers tend to fluctuate from season to season in a relatively predictable annual pattern. These communities may have some species that hibernate during the winter season, thereby affecting the seasonal dynamics of the community. Nevertheless, the year-to-year composition and biomass estimates of a desert or forest community of small mammals

are likely to be more predictably constant than a community with *Microtus*.

By contrast, communities with *Microtus*: 1) often fluctuate greatly in numbers, not only from season to season but from year to year as well, mainly because of *Microtus*; 2) have proportionately more individuals active throughout the daylight hours as well as at night, which is largely due to the intermittent activity periods of *Microtus* (Madison, this volume; Shields, 1976); 3) have more predators focusing on them, because *Microtus* are relatively large among small mammals, often numerous, and available to diurnal as well as nocturnal predators; 4) have continuous activity because, although other community members such as *Zapus, Spermophilus,* and more rarely *Perognathus,* may hibernate, *Microtus* is active year-round; and 5) have relatively constant harvesting of vegetation because *Microtus,* with few exceptions, does not store food in caches. Communities with *Microtus,* then, often have high densities of small mammals that are active throughout the day, night, and year. Furthermore, during much of the year these small mammals tend to be dispersed more or less uniformly in the available habitat, in part because of spacing behavior described by Madison (this volume). In *M. xanthognathus* (Wolff, 1980) and *M. pennsylvanicus* (Madison, this volume), winter aggregations of voles conserve heat by communal nesting behavior but may suffer to a greater extent from predation because of it.

### *Effects of Density*

Certainly the greatest influence of *Microtus* on the community is due to its great numbers when populations are near or at peak densities (see Taitt and Krebs, this volume). Densities of 100–300/ha are typical of peak periods in the multi-year cycle, and more than 1,000/ha have been reported. Only when the high densities persist for months or occur outside the growing season is there a significant depletion of the covering and edible vegetation. Rodent plagues can occur under these conditions, as reported for *M. oregoni* in 1957, when densities of 4,500–6,500/ha were estimated in agricultural fields in Oregon (Fed. Coop. Ext. Serv., 1959). Even at moderately high densities, it seems likely that the community of small mammals must be adversely affected, probably in many ways. As densities increase, suboptimal habitat is colonized by *Microtus.* The consequences of such habitat expansion rarely have been measured, except in the extreme case of house-mouse populations going

to extinction as a result of successful colonization and subsequent population explosion of *M. californicus* on Brooks Island (Lidicker, 1966). Nevertheless, at high *Microtus* densities, most other small mammal species in the community will be affected somehow, either directly through interference competition for space or perhaps even for food, or indirectly through a physical alteration of the habitat as a result of partial denuding of vegetation, extensive digging of soil surface, and almost certainly by focusing predators on the large biomass of prey available in that habitat. It seems unlikely that a high biomass of *Microtus* would have a positive or beneficial impact on any species of small mammal, unless, as some have speculated, *Blarina* is a predator of nestling and young voles (Eadie, 1952).

### *Effects of Large Body Size*

Not only is *Microtus* often abundant, but it is usually the largest small mammal species in the community, especially grasslands. Large body size accentuates the effects of numerical dominance and may help to promote the dominating influence of *Microtus* in many communities. For example, large body size in small mammals often is associated with large litter size, thereby contributing to species density and biomass. Also promoting the ability to produce large litters is their high metabolic rate, higher than predicted by the Kleiber curve (Kleiber, 1961). The high metabolic rates that promote rapid body growth, early maturity, and large litters, often in rapid succession, require the rapid conversion of grass into small mammal biomass. McNab (1980) speculated that because natural selection tends to favor as high a metabolic rate as the diet will permit, a species with a high metabolic rate potentially will be more successful than a competitor with a lower metabolic rate. In the community context, this may mean that *Microtus* has an edge over other species primarily because of its high metabolic rate. In sum, these factors combine to contribute to the influential position of *Microtus* in many small mammal communities.

### *Effects on Community Succession*

Because high populations of *Microtus* often are associated with herbaceous vegetation of early stages of secondary plant succession, it might be expected that voles would influence the nature and rate of changes in plant communities. If that influence is real, then we would predict a concommitant secondary effect on succession of the

small mammal community. Unfortunately, there is almost no information on the influence *Microtus* has on the dynamics of plant succession. Unless the climax vegetation is tundra or grassland, *Microtus* is a transitory species, present only in early to middle seral stages. For example, Wetzel (1958), who studied biological succession on abandoned strip mines in Illinois, found that *M. ochrogaster* was absent during the initial revegetation stages when annuals dominated the vegetation, but became the dominant element of the small mammal community after grasses and woody perennials achieved dominance of the plant community. Prairie voles were abundant only for about 20 years, and they disappeared from the area when the deciduous trees achieved approximately 65% of the plant coverage.

When forests are cut, significant and rapid changes in the vegetation composition occur. Herbaceous species tend to dominate for a few years, creating a habitat in which one or more species of *Microtus* often comes to dominate the small mammal community. Kirkland's (1977) study in the northern Appalachian forests demonstrated the transitory nature of *Microtus* in the deciduous and coniferous forests there. *M. pennsylvanicus* and *Synaptomys cooperi* were absent in both forest types that had not been cut for more than 25 years. After cutting, both microtines appeared, but they were absent after 5 years. *M. chrotorrhinus* was present at moderate densities in the 7- to 25-year-old forests, but increased significantly in both forest types after clearcutting and remained there for at least 15 years. Initial responses of the total small mammal community included increases in density and in community diversity as well as shifts in relative abundance of individual species and trophic groups. Krefting and Ahlgren (1974) reported similar responses by the small mammal communities following forest fires in Minnesota.

Gashwiler (1970) obtained similar results in a coniferous (mostly Douglas fir) forest in Oregon, where *M. oregoni* appeared in the clearcuts 1 year after cutting and increased to moderate densities by the fourth year, then decreased slightly but remained appreciably higher than populations in nearby virgin forest. *M. richardsoni* occasionally was taken on the clearcut but apparently did not establish a resident population there.

The ability of *Microtus* to colonize productive habitat quickly was demonstrated clearly by Grant et al. (1977), where only a single *M. ochrogaster* was trapped during 15,000 trap-nights in a grazed pasture and none was present on the nearby experimental grids prior to the application of irrigation water and nitrogen. Yet, within

a few weeks a rapidly growing population of prairie voles was present in the dense vegetation that resulted from the experimental treatment. Although *Microtus* species can recolonize quickly after such disturbances as mowing (Getz, 1970) or grazing (Birney et al., 1976), succession of a small mammal community following the plowing of a prairie and its subsequent abandonment has not been studied adequately. In wetter tallgrass prairie, grasses undoubtedly would reappear more quickly than in drier mixed or shortgrass prairies, which would have a longer period of domination by annuals. Here, omnivores such as *Peromyscus maniculatus* probably would dominate for several years before *Microtus* would invade and come to dominate as the climax grasses reappeared. Succession in this case would lead to *Microtus* as the long-term dominant rather than as the transitory species it is when forest is the climax vegetation of the region.

Because the experiments excluding *Microtus* from some plots but not others have not been conducted, it is unknown whether *Microtus* influences the progression of plant succession at a given location. Although these exclosure studies would be long-term studies of plant and animal community dynamics, we believe that the influence of *Microtus* on the process can only be evaluated through such experimentation.

## *The Role of* Microtus *in Small Mammal Communities*

The major role of *Microtus* in the small mammal community is as principal herbivore in almost all plant communities where it lives. As grazers, primarily of stems and leaves, *Microtus* has the potential to alter plant communities and indirectly to help determine the habitat structure and resources available to other syntopic small mammals.

*Microtus* is usually the dominant primary consumer among the small mammals living in grassland and tundra communities. Species of *Microtus* that have been studied for their dietary selection eat mostly vegetative plant parts. Zimmerman (1965), studying *Microtus* food and habitat in western Indiana, reported that *M. ochrogaster* ate proportionately more roots and seeds (18.8% of volume) than did *M. pennsylvanicus* (0.4% of volume). These two species ate insect material at the rate of 4.7 and 3.6%, respectively. Each

species consumed a small amount of *Microtus* flesh and subterranean fungi, but about 93% of the volume of food was vascular plants, mostly stems and leaves. Zimmerman (1965) noted that *M. ochrogaster* took the most common plants in greatest frequency (also reported by Fleharty and Olson, 1969, and Martin, 1956, in Kansas), but some plants, especially the somewhat aromatic *Ambrosia, Aster,* and *Solidago,* generally were avoided. Meadow voles in Indiana (Zimmerman, 1965) ate fewer kinds of plants but were similar to prairie voles in relying heavily on the common species. M'Closkey and Fieldwick (1975), who evaluated the foods of coexisting *Peromyscus leucopus* and *M. pennsylvanicus,* found that the former ate 74% and the latter 8% insect material, the remainder being combinations of dicots, monocots, subterranean fungi and, for *Microtus* only, ferns (6%).

Food selection by *M. xanthognathus* in black-spruce forest has been studied by Wolff and Lidicker (1980) and West (1979), both in interior Alaska, and by Douglass (1976, 1977) in Northwest Territories. In Alaska, more than 85% of the diet was grasses and berries; in Wolff and Lidicker's (1980) study, a large proportion (37% of the volume) was *Equisetum* (horsetails). Douglass and Douglass (1977), who examined the summer foods of *M. xanthognathus,* reported the following composition of 629 piles of cuttings: 89% *Carex* spp., 5% *Rumex,* 3% *Calamogrostis,* 2% *Vaccinium,* and 1% *Equisetum.* Thus, despite their use of taiga as habitat, taiga voles ate little woody material but did rely heavily on the grasses and other herbs for food. This dietary selection possibly accounts for the fact that the densities of *M. xanthognathus* are much greater than have been reported for either *M. pinetorum* or *M. chrotorrhinus* in other forest environments.

Stomach content analyses, coupled with a census of the available foods, are badly needed to learn more of the details of the role of *Microtus* as consumers. Studies of food habits during periods of gradual community change may be especially revealing in explaining why *Microtus* often is present only for a relatively brief period in early seral stages. During biological succession, if *Microtus* persists in relying almost entirely on the ever-diminishing grasses and herbs, the replacement of *Microtus* by *Peromyscus leucopus, P. maniculatus* (woodland subspecies), or *Clethrionomys* spp. may be related more to diminishing food resources than to competition with these rodents. Although the water- and nitrogen-supplementation

experiments of Grant et al. (1977) suggest a strong positive association between primary production of grasses on the Colorado shortgrass prairie and secondary production of *Microtus,* additional experimental studies are needed, including those of forest-dwelling *Microtus,* to demonstrate a link between the biomass of herbaceous vegetation and that of *Microtus.* The abundance of *M. pennsylvanicus, M. oeconomus,* and especially *M. xanthognathus* and vegetative cover values correlated positively in early successional stages of burned-over black-spruce forest in Alaska, but correlated negatively in advanced successional stages (West, 1979).

Relatively few attempts have been made to examine the biomass of small mammal communities, and to measure the changing role of the member species from year to year. Pruitt (1966) was unable to find synchrony between sample plots of either species or number of individuals. However, when he considered biomass per sample plot (Pruitt, 1968), he did detect synchrony among the biomasses of small mammals. Pruitt's studies, conducted over 8 years in different regions of Alaska, evaluated the differential contributions of two species of *Sorex,* two of *Microtus,* and those of three other microtine rodents. Pruitt (1968) interpreted these results to mean that ecosystem productivity "waxes and wanes in a regular progression." Chance, which he believed determined the "massive increase or decrease" of species, perhaps plays less of a role where the climatic extremes are not so severe. Martin (1956) looked at the relationship between plant production and the biomasses of *M. ochrogaster* and *Sigmodon hispidus,* but he only reported values for a single month; repeated values would have permitted an evaluation of the changing roles of the two herbivores to determine whether *Microtus* contributed relatively more during the cool months and *Sigmodon* more in the warm months.

Grant et al. (1982) compared the effects of habitat perturbation (grazing) on the small mammal biomass in different grassland types, using treatment and control grids. The detrimental effects were substantially greater in the tallgrass prairie (where *M. ochrogaster* and *Sigmodon hispidus* shared the herbivore role) than at the bunchgrass or shortgrass sites. Grant et al. (1982) suggested that seasonal and year-to-year fluctuations in the biomass of small mammal species cause a high variability in the community biomass of a site, and they argued that biomass changes are characteristic of many types of North American grasslands (French et al., 1976; Grant and

Birney, 1979). These variations are similar to what Pruitt (1968) called "fortuitous" events that determine the changing contributions of individual species from year to year at the same location. At the tallgrass site, Grant et al. (1982) found that grazing resulted in an increased contribution of *Spermophilus* and *Peromyscus maniculatus bairdii* to small mammal biomass; the contribution of *M. ochrogaster* and *Sigmodon* to biomass dropped by 90% on the grazed plots.

French et al. (1976) evaluated the energetics of small mammals of grassland ecosystems in the central U.S. Except for 1 year on a desert grassland, small mammals consumed less than 10% of the available herbage foods. By contrast, a high proportion of animal food was eaten at many sites in different years. These authors speculated that seed-eaters are more K-selected (they exhibit hibernation and torpor) and have social mechanisms and body-size differences to reduce competition. They argued that these adaptations contributed to their success relative to the grass-eaters in shortgrass prairie, where *Microtus* is abundant only on experimental plots in which water and nitrogen stimulated growth of grasses (Grant et al., 1977).

Golley (1960) measured energy flow in a grass-*Microtus*-*Mustela* system in Michigan. He estimated that *M. pennsylvanicus* consumed only 1.6% of the energy available to it, and that the weasel consumed 31% of energy available in the form of *Microtus*.

The presence of *Microtus* in a community often results in a significant physical alteration of the environment because they construct runways and burrows and extensively clip herbaceous vegetation. Pearson (1959), using photographs, showed that many other species of small mammals used runways built and maintained by *Microtus*. Digging activities of *Microtus* may create exposed soil substrates needed by seeds to germinate. Effects of grazing by *Microtus* are disputed and undoubtedly are variable; grazing may stimulate some plants to produce new vegetative growth but also may seriously or mortally wound other plants. Experiments to evaluate critically the role of *Microtus* in altering the habitat, using exclosures and measured densities of voles, have not been conducted at even a single location, to our knowledge. This is certainly an area of research where large contributions can be made in our understanding of the role of *Microtus* in the small mammal community and in the ecosystem.

## *Conclusions and Perspectives*

*Microtus* is found in most grassland and tundra communities, and to a lesser extent in forest communities north of 35°N. As many as four to six species of *Microtus* may be broadly sympatric in some regions, such as in the western U.S. *Microtus* often is both the largest and the most numerous small mammal, and the genus may contribute 90% or more of the small mammal biomass per unit area. Exceptions to this trend can be found in marginal habitats, in the usually brief periods of low density in population cycles, in certain successional stages, and in forests. Predators may focus on *Microtus* where it is abundant, and *Microtus* influences the small mammal community in other ways. *Microtus* eats plant parts almost exclusively and is usually the dominant primary consumer.

Despite this prominent position in its community, *Microtus* rarely has been evaluated, and almost never studied, in the community context. Sometimes *Microtus* and one or two syntopic microtines are examined, either for evidence of competition or of synchrony of population cycles. In some instances, the composition and relative numbers of small mammals in the community are reported, permitting the reader to assess the potential effect of coexisting species on *Microtus*. Occasionally authors make it clear that non-microtines were or were not permanently removed from the study grids, but in many cases no statement is given about the occurrence of other species. Although it is understandable that microtine population ecologists may foresee little immediate benefit from the trapping, tagging, and handling during each trapping period of dozens of *Peromyscus, Sigmodon, Reithrodontomys,* or other species, an understanding of the dynamics of these species may be crucial to explaining microtine cycles, especially if Lidicker (1973, 1978) is correct in his assertion that many factors are involved in population regulation of *Microtus*. More importantly, neither the influence of *Microtus* on the small mammal community nor the role of *Microtus* in the ecosystem can be evaluated critically until all small mammals are examined together.

One thing we have learned, more than any other, from writing this chapter, is that the study of *Microtus* in the community context is a potentially fertile area of research. *Microtus* typically is not present in community studies of small mammals in desert (Brown,

1973, et seq.) nor in eastern decidious forest (Dueser and Shugart, 1978, 1979). Among those studying *Microtus,* only West (1979) has used Dueser and Shugart's technique of measuring vegetation structure and predicting which species will use which components of the physical habitats. Except for Grant's (1969, et seq.) experimental studies of competition with field populations of *M. pennsylvanicus* and one other species, planned experiments have not been conducted to learn more details of the respective roles of the four to six small mammal species in grassland and tundra communities. The study of mammalian community ecology in these plant communities will not be easy, in part because the number of *Microtus* often is much greater than that of all others. On the other hand, when numbers of *Microtus* are low, poor trapping success may cause the investigator to question whether or not to continue the study. Perhaps the best descriptive studies could be conducted in plant communities that are in transition; for example, large grasslands that grade into shrubby ecotones and then into young and old forest could be ideal. Here it would be possible to see the changing role of grassland *Microtus* as the woody elements increase to dominance. Leaps of insight will be possible using perturbation experiments, especially large and well-replicated ones in which more than two species can be evaluated simultaneously. Finally, some investigators, such as West (1979), have the necessary detailed information from fairly long-term studies to meld what may have been designed as multiple population studies into reports of small mammal communities with *Microtus*. Such reports would be extremely valuable in providing direction for the descriptive and experimental studies that are necessary if we are to learn the true influence and role of *Microtus* in small mammal communities.

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